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Trichinellosis: the zoonosis that won't go quietly

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Abstract

Trichinellosis, is normally not included among those regarded as emerging zoonoses because it has been a public health threat for more than 150 years. However, its dramatic re-emergence in many areas around the world over the past 10–20 years, inspite of a century of veterinary public health efforts to control and eradicate it, justifies it being included in this group. The reasons for this re-emergence are diverse, and include human pertubation and manipulation of ecosystems, war and political turmoil, rapidly changing food distribution and marketing systems, and even, surprisingly, rising affluence in developing countries. These influences, and their impact on the epidemiology of both domestic and sylvatic trichinellosis, are discussed, along with recommendations for confronting this altered status as a public health threat. © 2000 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

Keywords: Trichinellosis; Zoonosis; *Trichinella*; Public health; Epidemiology

1. Introduction

Trichinellosis persists in confounding scientists and public health authorities who, after 150 years of control efforts, have expected it to recede to an incidental mention in text books. Prior to the 1970's, human trichinellosis from infected pork had declined markedly throughout the world, particularly in Europe and the United States [1,2]. However, as shown in Table 1, trichinellosis is again a threat in both developed and the developing regions [9]. As examples, the incidence of human cases have increased 17 fold in Romania since 1983, 7-fold in Argentina from 1993 and 9-fold in Lithuania since 1989. In Serbia, porcine trichinellosis spread during the 1990s from four restricted foci to nearly a third of the country, and in China (Henan Pr.), prevalences in pigs increased from less than 1% in 1982 to 15% in 1990. Intimately related to this resurgence are important changes in the epidemiology of the zoonosis. Until recently, outbreaks predominantly resulted from consumption of *Trichinella spiralis*-infected pork in local, single-source outbreaks; however, increasingly, the mass-marketing of meat can disseminate the parasite throughout a large population. Also of importance is the growing proportion of outbreaks caused by sylvatic *Trichinella* species, either directly through game meat or through spill-over to domestic animals. Recent reports also indicate that infected herbivores other than horses (i.e. sheep, goats and cattle) have been the source of outbreaks, a new variation on the traditional model of trichinellosis epidemiology. The emergence or re-emergence of a parasite like *Trichinella* results from a change in either the ecology of the host, the parasite, or both, because zoonotic parasites exist within a continuum among wild animals, domestic animals and human populations [40]. Underlying causal factors which lead to changes include encroachment from human activity in the form of agricultural intensification and environmental alterations, translocations of animal populations, human travel, and export of food. The re-emergence of trichinellosis in recent years reflects many of these forces. Coupled to this is the growing recognition of the important role played by the sylvatic *Trichinella* species, and the impact of human activities on their ecology. As a consequence, this resurgence has sparked, along with heightened public health concerns, an intensification of research. Investigations on the systematics of *Trichinella*, especially, have revealed much about the changing epidemiology of this zoonosis.

The development in general evolutionary and systematic biology, beginning in the 1960s, has helped provide new insights into the genetics of *Trichinella,* producing both a new taxonomy for the genus (Table 2) and the development of powerful molecular tools for identifying species [41]. These new tools have also greatly enhanced the ability to detect infection, thereby increasing our ability to accurately

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Table 1
Recent outbreaks of trichinellosis, by geographic region and country

Geographic region/country	Year	Number of cases	Source	*Trichinella* species	References
North America					
Canada	1989	49	Polar bear, walrus, wild boar	*T. nativa T. spiralis*	[3,4]
Mexico	1991–1995	282	Pork	*T. spiralis*	[5]
United States	1991–1996	230	Pork, wild game	*T. spiralis, T. murrelli,* T6	[6,7]
South America					
Argentina	1990–1999	5217	Pork; mountain lion	*T. spiralis*	[8,62]
Europe					
Bulgaria	1993–1995	2335	Pork, wild boar	*T. spiralis*	[9,10]
Byelorussia	1987–1994	268	Pork, game	ND[a]	[11]
Croatia	1994–1996	425	Pork	*T. spiralis*	[10]
	1997–1998	1024	Pork	ND	ITRC[b]
England	1999	8	Pork	*T. spiralis*	[12]
France	1992–1999	27	Wild boar	*T. britovi*	[13,14,15]
				T. pseudospiralis	[16]
	1991–1998	1097	Horse	*T. spiralis*	[17,18]
Germany	1990–1998	82	Pork	*T. spiralis*	[19]
Italy	1990–2000	621	Horse	*T. spiralis*	[20]
		13	Pork	*T. britovi*	
		44	Wild boar	*T. britovi*	
Latvia	1995–1997	156	Pork, wild boar	ND	[10]
	1999[c]	40	Not reported	ND	
Lithuania	1993–1999	1290	Pork	*T. spiralis*	[21,22,23]
Poland	1993–1997	352	Pork, wild boar	*T. spiralis*	[10]
Romania	1990–1999	16712	Pork	*T. spiralis*	[10,24,99] ITRC[b]
Russia	1993–1994	1720	Pork; game	ND	[9,10]
	1995–1997	1432	Pork		
Serbia	1995–1998	1806	Pork	*T. spiralis*	[10,25]
	1999	559	Pork	*T. spiralis*	
Slovakia	1998–1999	336	Dog	*T. britovi*	[26]
		30	Game	ND	[10]
Spain	1993–1995	98	Pork	*T. spiralis*	[9,27]
	1995–1998	192	Wild boar	*T. spiralis*	[10,28]
Asia					
China[d]	1964–1999	23004	Pork, mutton, beef, dog, game	ND	[29]
China (Henan Prov.)	1992–1995	467	Pork, mutton	ND	[10]
	1995–1996	>600	Pork	ND	[30]
	1997	47	Mutton	ND	[31]
China (Hubei Prov.)	1982–1998	2654	Pork, goat, dog	ND	[32]
China (Yunnan Prov)	1964–1998	20101	Pork, bear	ND	[33]
Lebanon	1982	>1000	Pork	*T. spiralis*	[34]
	1997	200	Pork	*T. spiralis*	[35]
Kamchatka	1997	49	Pork	*T. pseudospiralis*	[36]
Korea	1998	3	Raccoon dog	*T. spiralis*	ITRC[b]
Thailand	1996	45	Pork	*T. spiralis*	[37]
	1994	59	Pork	*T. pseudospiralis*	[38]
Australia					
Tasmania	1994	1	ND	*T. pseudospiralis*	[39]

[a] Not determined.
[b] International *Trichinella* Reference Centre, Rome, Italy (*www.simi.iss.it/trichinella/index.htm*).
[c] Report from L. Viksna, Latvijas Infektologijas Centrs (pers. commun).
[d] Summary from 12 provinces/ autonomous regions/municipalities.

trace the source of human outbreaks. This has been a key factor in the growing recognition of the importance of sylvatic species in this disease's epidemiology and of alternative transmission paths for *Trichinella*. Examples of the latter are the still somewhat enigmatic transmission of the parasite to horses [27], and reports that domestic animals (sheep, cattle, dogs) may also serve as a source of human infections [31,42].

Table 2
Trichinella species and related genotypes, their natural cycles, main hosts, and distribution areas

Trichinella species or genotype	Cycle	Main hosts	Distribution area
T. spiralis	Domestic and Sylvatic	Swine, carnivores, rats	Cosmopolitan
T. nativa	Sylvatic	Carnivores	Arctic and subarctic regions
Trichinella T6	Sylvatic	Carnivores	Southern Canada, northern USA
T. britovi	Sylvatic	Carnivores	Temperate areas of the Palearctic region
Trichinella T8	Sylvatic	Carnivores	South Africa and Namibia
Trichinella T9	Sylvatic	Carnivores	Japan
T. murrelli	Sylvatic	Carnivores	USA
T. nelsoni	Sylvatic	Carnivores	Africa south of the Sahara
T. pseudospiralis	Sylvatic	Mammals and birds (carnivores and omnivores)	Cosmopolitan
T. papuae	Sylvatic, domestic?	Swine	Papua New Guinea

It is clear that the frequent breakdown in veterinary public health systems, and the associated re-emergence of zoonotic pathogens, in regions such as eastern Europe, is an important consequence of political upheaval, war and drastic economic fluctuations. Demographic and cultural behavioral changes are also important causes of the introduction of *Trichinella* to new locations. The recent pork-derived outbreak in London [12] and the importation of infected horses into France and Italy resulted from such cultural and political factors.

The economic impact of a relatively low prevalence zoonosis such as trichinellosis is often overlooked, but it can be tremendous. As a result of mandatory inspection of the nearly 200 million pigs slaughtered annually, the European Union (EU) spends about US$ 570 million yearly for inspection for *Trichinella* [43]. The economic cost of swine and human trichinellosis in the United States (US) is also substantial (est. 1 billion US$ annually), primarily for health regulatory activities to prevent infection which includes the utility costs to treat pork (freezing, heating, curing, etc.) [44–46]. Such direct and indirect costs make trichinellosis one of the most costly of all parasitic zoonosis.

The epidemiological complexity of this zoonosis is only now becoming fully appreciated. This review explores this and includes an analysis of the most important causal factors, along with a status report on recent human outbreaks and their epidemiological features. The linkage between clarification of the difficult systematics of this genus and the illumination of the ecological features which govern the zoonotic potential of this parasite is emphasized. The importance of this new knowledge to the design of more effective veterinary public health measures will also be highlighted.

2. Important human influences

Because the basic transmission path of this parasite is relatively simple and because various control measures have been in place for over 150 years, it is surprising that this zoonosis is re-emerging. Until recently, the concept that the main source of human trichinellosis is the domestic pigs has been deep-rooted, leading most people working in public health to continue to teach and write text books expounding this narrow view. This adversely affects the approach of veterinarians and epidemiologists to its control, chiefly because it causes the role of the sylvatic cycle to be frequently overlooked. In developed countries, the general belief that trichinellosis was only a problem up to about the 1960s and that today consumers are protected by both meat inspection carried out at the slaughterhouse and the eradication of this infection from industrialised pig farms, has influenced public health priorities [47]. In some cases, this has resulted in relaxation of controls at the slaughterhouse. The high degree of success achieved by the 1960s in the control of *Trichinella* infections and the disappearance of this pathogen from domestic pigs in industrialised countries may also mislead inspectors into a level of complacency. Most of the technicians in charge of the control for *Trichinella* in European slaughterhouses have never seen a larva of *Trichinella*!

Improved detection has played an important role in recognising the persistence and spread of this zoonosis. The great improvement in immunodiagnostic tools has resulted in recognition that infection is at a higher prevalence among humans and animals than expected. Prior to the 1980s, most diagnoses were based on clinical signs and symptoms [44]. The increased ability to diagnose infections in humans has led to the discovery of new sources of infection and new routes for the introduction of *Trichinella* parasites into the domestic habitat.

Another contributing factor is the global increase in animal and meat trade, which has transferred *Trichinella* from endemic to non-endemic regions, where the veterinary services are often not familiar with the infection. The frequent importation of *Trichinella* infected horses from eastern European countries and from North America and Mexico have been the source of more than 3300 human infections in France and Italy [48]. Modern mass marketing of food can also change the traditional trichinellosis outbreak paradigm from that of a localised, single source type to a diffuse, broadly spread risk [19].

Changing livestock production practices, especially the increasing number of ecological (or organic) pig farms, has increased the risk of transmission of *Trichinella* from wildlife to domestic animals. The increasing use of protein of animal origin in the feeding of herbivores is possibly the basis of horse and reported bovine and ovine infections. Amazingly, in some EU countries, pigs reared on organic farms intended for personal or familiar consumption are not required to be inspected at normal EU standards.

Human migration along with the introduction of new food habits and risky animal rearing practices to other countries have also contributed to an increase in human and animal infections. Outbreaks due to the consumption of pork sometimes occur in communities of people emigrating from countries where, although domestic trichinellosis is present, risky food habits are culturally well-established [49]. In South-Central America, domestic trichinellosis is present where Spanish and sometimes German dietary customs prevail (i.e. Argentina, Bolivia, Chile and Mexico); however, this infection has never been reported in Brazil, where Portuguese immigration prevailed. This is understandable when it is recognised that domestic trichinellosis is still widespread in Spain, and was widespread in Germany until the 19th century, whereas it has never been reported in Portugal. On the other hand, a number of outbreaks have occurred in the US among southeast Asians who have immigrated from areas where trichinellosis is rare. These outbreaks typically result from preparation of native dishes of uncooked or partially cooked pork [2,49].

Human behaviour can markedly influence the transmission patterns of *Trichinella* in other ways. For example, in the northern hemisphere, *Trichinella* infections in humans occur mostly between December and February, when the number of pigs slaughtered for family consumption increases (this is also the peak hunting season). The reverse is true for the southern hemisphere, (e.g. Argentina and Chile), where the incidence rises in the winter period of June–August. The increased consumption of game meat, the increased number of farms breeding wild animals for sport hunting, and the increased number of wild boar populations (following reductions in human rural populations) represent increased risk. This has resulted in increased opportunity for the transmission of *T. spiralis* from the sylvatic to the domestic habitat. Related risk factors are the increasing numbers of hunters, and their tendency to leave game carcasses in the field (which increases the exposure of this infection to wildlife [50,51].

3. Current worldwide status as a zoonosis and the relationship to regional factors

The new taxonomic scheme of ten *Trichinella* genotypes (Table 2), seven of which are at the species level (*T. spiralis*, *T. nativa*, *T. britovi*, *T. pseudospiralis*, *T. murrelli*, *T. nelsoni* and *T. papuae*) allows important biological and epidemiological information on trichinellosis to be organised into a more understandable and predictable epidemiological pattern [41]. The cosmopolitan distribution of *T. spiralis* over five continents is unique because this parasite has been introduced passively by humans from Eurasia to North and South America, Africa (Egypt), and New Zealand [41]. Most regions feature a more restricted array of *Trichinella* species.

No region has experienced a more marked change in the threat of trichinellosis than that of eastern Europe (Table 1). In Romania, the incidence of infection has increased 17 fold since 1983, making trichinellosis the country's most important parasitic disease [24]. This is also reflected in the 50% increase in pig prevalence (to 0.15%) that occurred between 1991 and 1993. This upward trend is due, at least in part, to changes in pig production practices that accompanied the country's shift to private ownership of agricultural production and a reduction in veterinary public infrastructure. The disastrous impact of war and population migration on a zoonosis like trichinellosis is especially evident in countries such as Croatia and Serbia (Table 1). In Serbia, the presence of porcine trichinellosis has, over the last few years, spread from four restricted areas to nearly 30% of the region [25]. Changes in pig production practices also appear to account for much of the increased human and pig infections in Russia during the 1990s [11]. For similar reasons, the incidence of trichinellosis in Lithuania increased nine fold from 1989–1994 (to 19.2 cases/100 000) [21]. In eastern Europe, this zoonosis is also characterised by the emergence of important non-pork sources of infection. Dog meat has been implicated in an outbreak in Slovakia, and the risk from wild game such as wild boars is substantial throughout the region [26]. This epidemiology also underscores the importance of the sylvatic species, especially *T. britovi*. Dog meat has also been implicated in an outbreak in Kazakhstan, affecting 17 people, six of whom were admitted to hospital [10]. Of particular interest are the reports of pig infections with *T. pseudospiralis*; in Kamchatka, one-half of pork-derived human infections are attributed to this species [36].

The high prevalence in domestic and wild animals in eastern Europe has increased the risk of importing infected meat in the EU. A recent outbreak in London resulted from the importation of sausages from Serbia [12], and the origin of most of the horses responsible for the large outbreaks in Italy and France in recent years (Table 1) has been the east European region [48]. Over the past decade, horse meat has become the major source of trichinellosis in the EU, especially in France and Italy, accounting for more than 50% of *Trichinella* infections in humans [48]. Surprisingly, the import of wild boars from the US has been implicated in an outbreak in France in 1999 (Table 1).

Recent surveys suggest that trichinellosis has disappeared from Denmark both in domestic and sylvatic animals. Until recently, there have been no reports in the British Isles of these parasites in domestic animals or humans since 1969. However, the hypothesis that these countries are *Trichinella*-free needs to be supported through epidemiological surveys involving all potential hosts. In addition to these countries, there are large regions in other countries (generally lowlands) where both domestic and sylvatic cycles are absent. For example, there is enough data available to consider the northwest regions of France, the Po valley and other plains in Italy, and the islands of the Mediterranean Sea *Trichinella*-free (Corsica, Sardinia, Sicily, etc.) [43]. In the Extramadura of Spain, however, the high prevalence in wild boars (0.48%) is a risk factor for domestic swine production [52]. In southern Finland, the prevalence in wild boars is reported to be 1.3% [53]; in contrast, in France, infection in wild boars ranges from 0.0002–0.003% [47].

The rising importance of wild animals as a direct and indirect source of domestic and human trichinellosis is also illustrated by the epidemiological changes experienced in the US. The proportion of reported cases associated with wild game increased from 27–42% during the period 1987–1996 [6]. This coincides with a dramatic decrease in swine prevalence [7]. Numerous studies have implicated the access of pigs to wildlife reservoirs as a major risk factor [7,54–56]. A recent outbreak of trichinellosis involving cougar meat underscores the need to change public perception regarding potential sources of infection [57].

The highest prevalence of human trichinellosis in Canada occurs in the eastern arctic, northern Quebec and the Rocky Mountain regions of British Columbia and Alberta [58]. Since 1971, approximately 72% of reported human cases originated in the Northwest Territories and Quebec, where the infection rate has been 200 times the national rate. Although domestic trichinellosis appears to have greatly decreased in Canada, sporadic cases are still reported in swine (Nova Scotia) [58] and in domesticated wild boar (*Sus scrofa*) (Ontario) [3]; the latter was the source of infection for 24 persons in 1993. In the period 1991–1997, the mean number of annual trichinellosis cases in humans was 18.2 ± 13.2 (range 3–49); however, because only the most severe cases are likely to be reported [4], the actual incidence is unclear.

In recent years, more than 1000 human infections have been documented in Mexico with a mortality rate of 1.5%. However, these cases are probably only the tip of the iceberg due to the lack of widely available adequate diagnostic tools. In the period 1991–1995 alone, 282 human infections were officially reported in seven outbreaks [59]. A recent study of 1050 serum samples collected from individuals living in different areas of Mexico suggested a prevalence of 12% [10]. Porcine trichinellosis is endemic in at least 11 federal districts, but there is little actual data on the incidence in swine due to the fact that inspection is carried out only in federal abattoirs, which are supplied with pigs mostly from industrialised farms. Serological surveys of backyard pigs in different areas of the country revealed a seroprevalence ranging from 1–20% [5]. The widespread poverty in Mexico occasions the consumption of non-inspected meat from backyard pigs fed on garbage, thereby increasing the risk of human infection. This high contamination of the farm habitat is also a risk factor for horses; the parasite has been detected in four horses and a seroepidemiological study of horses revealed a prevalence of 10% [60]; serodiagnosis in horses is only a conservative estimate of trichinellosis prevalence because infected horses frequently do not produce detectable antibodies [61].

Domestic trichinellosis is endemic in Argentina, but in recent years there has been a marked increase in both human and pig infections (Table 1). This zoonoses occurs mainly in four provinces, Buenos Aires, Cordoba, Neuquen and Santa Fe [62]. In the period 1990–1999, 5217 human infections have been documented; this may be an underestimate because many moderate infections may have been misdiagnosed [62]. In the province of Buenos Aires the number of infections in humans increased from 44 to 543 in the period 1991–1996, while the number of foci of porcine trichinellosis increased from 11 to 75 from 1992 to 1996. Infected animals generally originated from small farms.

In 1991, domestic trichinellosis was detected for the first time in pigs from the Bolivian Altiplano by serology [63]. The rate of swine infection in Chile, however, has decreased. These data concern only pigs slaughtered in public abattoirs and do not include pigs slaughtered at home; such backyard pigs are generally of the highest risk to humans. For example, in a rural locality south-west of Santiago, Chile, *T. spiralis* infections in home-raised pigs may range up to 4% [10].

Increasingly, trichinellosis is being reported from eastern and western Asia [64]. In western Asia, there have been two large outbreaks since the 1980s in Lebanon [34,35]. The increasing incidence of trichinellosis in China illustrates very well the influence of socio-cultural and economic changes. In Henan Province, for example, prior to 1984, trichinellosis was rarely reported; however, since 1992, there have been seven outbreaks [65]. A recent serosurvey of humans in this province revealed an overall prevalence of 4.7% [66]. The increase in human infections appears to be directly related to an increase in swine prevalence, which rose from 0.44–0.86% in 1982 to 3.1–15% in 1990 [30]. Of particular epidemiological interest is the role of mutton, which was discovered to be a source of infection. A factor in this rising occurrence of trichinellosis in China is the improving economic status of the population, which has led to a growing preference for so-called 'scalded' pork and mutton dumplings. This food (often undercooked);-serves not only as a source of infection for people but also for pigs, sheep, and cattle fed table scraps [42,67]. The rising income and changing food preferences of the population, is also of importance in that it produces a link between incidence and education level [30]. This changing epidemiology is an excellent example of the need to expand programs on health education and food safety in regions where major economic and social change is underway.

In Indonesia, domestic trichinellosis and human infections have been documented only in the island of Bali, probably because it is the only region of the country where most of inhabitants are non-Muslim [68]. Trichinellosis probably also occurs in Kampuchea, Laos, Vietnam, and Burma, but information is fragmentary and there are no official reports on this infection. In Thailand, *T. spiralis* has caused outbreaks in humans, domestic and wild pigs and dogs [37]. Recently, *T. pseudospiralis* from a wild pig was the cause of a human outbreak [38].

4. Distribution and role of sylvatic species of *Trichinella*

Both sylvatic species of *Trichinella* and synanthropic *T. spiralis* can be maintained in nature in wildlife for years, without any link with the human environment. However, improper human behaviour, i.e. the use of game animals as food for domestic animals, the poor management of organic (ecological) farms, where domestic pigs (and wild boars) come into contact with sylvatic animals, the habit of hunters of field-dressing game animals and use of carnivore carcasses as bait for other carnivores, increases game animal prevalences and the risk of introduction of infection to domestic pigs. This risky behaviour has established new foci of domestic trichinellosis, mainly due to *T. spiralis*, but sometimes also to *T. pseudospiralis* and *T. britovi*. Higher prevalences of infection in wildlife increase the chance of transmission of this zoonosis to humans especially when there is no veterinary controls. It follows that the knowledge of wildlife trichinellosis in a country or in a region, i.e. which animals are the main reservoir species and which *Trichinella* species are being transmitted is vital for any control program and can help veterinarian services to establish appropriate control strategies and controls at the slaughterhouse to prevent the transmission of this parasite to humans.

Three sylvatic *Trichinella* species have been identified in Europe: *T. britovi*, the etiological agent of sylvatic trichinellosis in most of the EU; *T. nativa*, the etiological agent of sylvatic trichinellosis in Finland and in some areas of central and northern Sweden; and *T. pseudospiralis* which occurs in wildlife of Finland, France and Italy. *Trichinella spiralis*, the etiological agent of domestic trichinellosis, may also occur in sylvatic animals. The transmission of these species can be characterised as occurring: (1) only in a sylvatic cycle (*T. britovi*, *T. nativa*, and *T. pseudospiralis*); (2) currently only in a sylvatic cycle (*T. spiralis*), although it may have formerly existed in a domestic cycle; and (3) in both a sylvatic and domestic cycle (*T. spiralis*) [43].

In most regions of the EU, the specific reservoir of the sylvatic cycle is the red fox, although in Finland it is also represented by the raccoon dog (*Nyctereutes procyonoides*) [53,69]. Mustelids (badger, *Meles meles*; beech marten, *Martes foina*; etc.) and other carnivores (bear, *Ursus arctos*; lynx, *Lynx lynx*; wolf, etc.) may also be infected, but because of their low population levels they probably have a limited role in the ecology of sylvatic trichinellosis. In the last ten years, *T. nativa* (frequently) and *T. britovi* (rarely) have been reported in the red fox of Norway; *T. nativa* also occurs in polar bears from Svalbard islands [10,70].

The increase in wild boar populations in Europe in the last 20 years has led to increased consumption of this game in France, Germany, Italy and Spain and has resulted in an increase in human outbreaks (Table 1). In Estonia, although domestic trichinellosis is very rare, the prevalence of infection in wildlife is high: 79.4% in wolves, 50% in raccoon dogs, 47.4% in lynxes, and 42.1% in red foxes. Meat from wild animals is the main source of *Trichinella* infection for humans [71].

In Canada, three genotypes (*T. spiralis*, *T. nativa* and *Trichinella* T6) have been identified. *Trichinella nativa* occurs in carnivores (polar bear, *Ursus maritimus*; arctic fox, *Alopex lagopus*; wolf, *Canis lupus*; and walrus, *Odobenus rosmarus*) from several regions. *Trichinella* T6 has been detected in a human and in a black bear (*Ursus americanus*) from Ontario [47]. Overall in the North American arctic regions, polar bears are the key component in the ecology of *T. nativa*; with prevalences as high as 60% being reported [72].

In a survey of 4,773 individuals of 19 mammal species in central and northwestern Ontario, Canada, *Trichinella* was found in 46% of fisher (*Martes pennanti*) and 3.4% of marten (*Martes martes*) [73]. Smith and Snowden [74] reported *Trichinella* in 2.7% of arctic foxes, 3.1% of red foxes, 7.9% of wolves, 0.4% of coyotes (*Canis latrans*), 0.8% of raccoons (*Procyon lotor*), 3.2% of lynx, 0.8% of bobcats (*Lynx rufus*), and 30% of dogs. Dies and Gunson [75] reported *Trichinella* in 56% of Canadian cougars (*Felis concolor*) and 2.9% of grizzly bears (*Ursus arctos horribilis*). On Prince Edward Island the occurence in wildlife of *Trichinella spiralis* was 0.96% for the red fox and 0.8% for the coyote [4].

Four *Trichinella* genotypes have been identified in the USA (lower 48 states): *T. spiralis*, both in domestic pigs and wildlife, *T. murrelli* and *Trichinella* T6 in wildlife, and *T. pseudospiralis* from a vulture in Alabama [76,77]. The agent of domestic trichinellosis, *T. spiralis*, has also been reported in black bear, raccoon, and skunk (*Mephitis mephitis*) in Pennsylvania, bobcat in Montana, coyote and opossum (*Didelphis virginiana*) in Indiana, red fox and domestic cat in Illinois, and wild boar of New Hampshire [51,55,78]. The prevalence of sylvatic trichinellosis varies among regions, with the highest rates in the eastern states and Rocky Mountain region, although comprehensive epidemiological surveys have not been carried out uniformly throughout the country.

In the Neotropic region, there are very few reports of *Trichinella* in wildlife [79,80]. Recently, *T. spiralis* was identified in two mountain lions, in a fox, and in an armadillo (*Chaetophractus villosus*) from Argentina [8,47]. This suggests that the sylvatic genotypes of *Trichinella* may not occur in this zoogeographical region.

Trichinellosis in sub-Sahara Africa does not appear to be an important public health problem; less than 100 human infections have been documented in Africa (Ethiopia, Kenya, Senegal, and Tanzania). In all cases, human infections were derived from the sylvatic cycle. The low level of *Trichinella* infection in sylvatic suidae, the practice of eating only well-cooked meat, and religious laws that forbid the consumption of pork, probably accounts for the rarity of human trichinellosis in this region [81]. Sylvatic trichinellosis appears to be confined to wildlife living in natural parks and protected areas, where the main reservoir is the spotted hyena (*Crocuta crocuta*), with prevalences from 43–85% [81]. The domestic cycle is present in Egypt, but human infections are rare and generally involve tourists. Sylvatic species of *Trichinella* have not been reported in wildlife from Africa north of the Sahara, although there are old reports showing the presence of *Trichinella* larvae in carnivores from this region.

There is little recent information on sylvatic trichinellosis in western Asian countries. In the past, trichinellosis has been reported in wildlife from Iran and Turkey, and human infections related to the sylvatic cycle have been documented [82].

Although there is no information on the sylvatic cycle in China, India, or South-East Asia, there have been two isolates of *Trichinella* in Japan, one from a black bear (*Ursus thibetanus japonicus*) and the other from a raccoon dog (*Nyctereutes procyonoides viverrinus*), both were identified as *Trichinella* T9 a new genotype related to *T. britovi* [83] (Table 2).

Wildlife trichinellosis has been documented in central Asia (Azerbaijan, Kazakhastan, Kirghizistan, Uzbekistan, Turkmenistan) in the wolf, red fox (*Vulpes vulpes*), corsac fox (*Vulpes corsac*), and golden jackal (*Canis aureus*), in which both *T. nativa* and *T. britovi* were recovered [84].

In the Australian region, *T. pseudospiralis* is widespread in Tasmanian wildlife (both mammals and birds) [85,86], and in a remote region of Papua New Guinea a new non-encapsulating species, *T. papuae*, was recently identified in domestic and feral swine [87]. There are only a very few old reports for the Indian subcontinent (between 1942 and 1983) on the presence of encapsulated and non-encapsulated trichinellas in synanthropic and sylvatic animals.

5. Ecological factors that increase the risk of trichinellosis

Until recently, the usual morphological criteria for separating helminth species have not proved adequate for *Trichinella* except for the non-encapsulated species. A number of PCR-based techniques have now been developed for differentiating *Trichinella* genotypes; the most useful appears to be multiplex-PCR [88] and PCR-RFLP [83]. These two PCR-based methods permit rapid identification of single larvae collected from human biopsies or from muscles of infected animals, a vital advantage for epidemiological investigations. The identification of the etiological agent can suggest the source of human infection and the origin of the infected animal. These powerful tools have been of immense value in the research on sylvatic trichinellosis and the role of these species as zoonoses and the ecological factors that determine their transmission.

Apparently, *T. britovi* and *T. nativa* only survive among populations of sylvatic carnivores living in natural undisturbed ecosystems such as remote wilderness, mountain areas, and national parks. An important factor in the distribution of these sylvatic species is the feeding behaviour of their primary hosts, particularly cannibalism and scavenging. These feeding habits occur more frequently in wilderness areas than in less remote areas because scavenging on animal carcasses is not attractive to carnivores living in or near human habitats where other food sources are abundant (e.g. human food refuse, domestic animal prey) [2]. In these latter areas, hunters may leave animal carcasses in the field, which has been shown to be responsible for a high prevalence (0.8%) of *T. britovi* infection in wild boars in Spain (Castilla and Leon) [9]. The prevalence of *T. spiralis* in wild boars is often high in related areas where traditional pig-rearing and poor sanitary conditions can create small garbage dumps containing *Trichinella*-infected pork waste near farms and villages. Currently, in the central and southern regions of the EU, sylvatic trichinellosis is most prevalent among foxes living either 400–500 m above sea level, or in protected areas (where the environment is less disturbed) [43]. In contrast, the lowlands are more likely to be *Trichinella*-free because of the greater impact of humans on the environment, which discourages wildlife. The cool mountain climate favours the survival of muscle larvae in host carrion for a longer period of time. The evolution of an ability of muscle larvae to persist in carcass muscles at low temperatures is likely influenced by the scavenging behaviour of the hosts of the sylvatic *Trichinella* species.

The more widespread distribution of sylvatic trichinellosis in the northern countries (Sweden and Finland) than in the central and southern regions of the EU, is again probably related to human impact on the natural ecosystem, which has been less intense than in southern Europe. In Austria, Belgium, southeast France, Germany, and southern Sweden, where the domestic cycle formerly existed, sylvatic carnivores may harbour both *T. spiralis* as well as *T. britovi*. The domestic habitat, however, is not a favourable environment for *T. britovi* (and sylvatic species in general) because its reproductive capacity in swine and synanthropic rodents is very low [47,89]. This results in a severe limitation on transmission of sylvatic species from wild animals to hosts associated with humans (e.g. domestic pigs and commensal rats). There are only a few reports on the occurrence of *T. britovi* and *T. nativa* in domestic animals: *Trichinella britovi* has been identified in domestic pigs from Byelorussia, Croatia, Estonia, France, Italy, Macedonia, and Spain, in domestic dogs from Italy, Kazakhstan, and Slovakia [47]; *T. nativa* has been detected in a domestic pig from China [90] and in domestic dogs in Kazakhstan [84]; *Trichinella pseudospiralis* has been detected in domestic pigs from Krasnodar, Kamchatka, and Tula regions of Russia [36], and *Trichinella papuae* has been found in five domestic sows from Papua New Guinea. In most of these cases, the source of pig infection was a fed carcass of a game animal, or the infected pig had been reared outdoors in remote areas where sylvatic trichinellosis was prevalent [47,55,56].

Overall, there appears to be an inverse relationship in western Europe between human population density and the presence of the sylvatic cycle [52], which is more common in areas where the average human population density is relatively low (56 in France or 73 in Italy inhabitants/km^2), than in regions with an average of 106 or more inhabitants/km^2.

Epidemiological investigations in arctic and subarctic regions have also revealed the influence of humans on the prevalence of trichinellosis in wildlife. The prevalence of *T. nativa* in Greenland's arctic foxes and polar bears is related to the hunting practices of the traditional Inuit culture [91]. Sled dogs, which may have prevalences up to 91%, are fed on remains from the hunt, often polar bear carcasses. In turn, dead dogs are frequently sunk in the tidal zone crevasses of sea ice, becoming available to scavengers. In northern Kazakhstan (Irtysh territory), the prevalence of *T. nativa* infection in the corsac fox population has been reported to be as high as 50% and is attributed to both the hunter's use of fox carcasses as fox bait and the improper disposal of carcass remains which can expose other foxes [98]. In European Russia, the prevalence of *T. nativa* infection in wolf populations from Tvier and Smoliensk regions is also very high (98.4%) and is related to the exposure of these animals to carcasses of domestic dogs and wolves, which are left in the forest or are used as hunting bait [10]. The use of animal carcasses as bait for bears in Canada has also been implicated as a source of infection for wild animals [73].

The lack of or the very low prevalence of *Trichinella* infection in wildlife in many areas of Canada, where the natural ecosystem is relatively undisturbed by humans, contrasts with the epidemiological picture observed in EU countries, where there is a positive relationship between *Trichinella* prevalence in wildlife and natural unaltered ecosystems [43]. It is possible that in these undisturbed areas of Canada, there is a higher dispersion of wildlife (low population densities) than in the more circumscribed areas of Europe, and, in this situation, carnivores with cannibalistic and scavenger behaviour, are less likely to encounter infected carcasses.

While the presence of *T. spiralis* in a domestic host (pig, rat) reveals the existence of the domestic cycle, the presence of a sylvatic *Trichinella* species in these hosts does not represent a persistent threat. Such infections represent a 'dead-end' for the sylvatic cycle because the sylvatic species cannot maintain themselves in a domestic cycle. In contrast, *T. spiralis* can invade the sylvatic habitat and become a threat to reinvade the domestic habitat when there is poor management of domestic animals (i.e. by pasturing domestic animals in remote wild areas or by feeding them remains of wild animals [43,55,56]. The transmission of *T. spiralis* from domestic pigs to sylvatic animals has been well documented [55]. Although the domestic cycle may be eradicated with appropriate strategies, the presence of *T. spiralis* among sylvatic carnivores represents the sword of Damocles for domestic pigs living in the same area.

Recently, it was reported that *Trichinella* larvae collected from muscles of crocodiles (*Crocodylus niloticus*) from Zimbabwe were able to infect both laboratory rats and domestic pigs [92]. Because this isolate has yet to be identified to species, its systematic status is uncertain. In an experimental infection of caimans (*Caiman sclerops*) with six species of *Trichinella*, no larvae were recovered from the muscles [93]. Experimental infections of snakes with *Trichinella* sp. were successful only when the reptile was held at high temperatures 37–39°C [94]. However, at these temperatures, reptiles can survive only for a short period of time, suggesting they cannot normally serve as hosts.

6. Control and surveillance

Although the re-emergence of trichinellosis derives from a complex of events such as socio-economic shifts, changing food preferences and human influences on the ecology of sylvatic species, the failure to establish and rigorously maintain proven and safe animal husbandry and food safety practices remains a major factor. The effects of changes in political and economic conditions frequently result in the weakening or loss of veterinary public health infrastructures, which serve to ensure safe animal rearing and slaughter practices, comprehensive meat inspection programs and effective meat processing procedures. In regions experiencing a resurgence of human trichinellosis associated with domestic animal production the immediate need is to improve on or re-establish these veterinary public health systems. To assist all national authorities in this, the International Commission on Trichinellosis (ICT) has recently issued a comprehensive guide for such actions: 'Recommendations on methods for the control of *Trichinella* in domestic and wild animals intended for human consumption' this publication can be downloaded from the ICT home page (www.krenet.it/ict). These recommendations provide detailed plans and technical guidance for safe animal production, and the slaughter testing of swine, horses, and wild game. It also includes actions to be taken when a positive sample is found (epidemiological follow-up, control measures, etc.). Procedures for effective meat processing to inactivating larvae (including cooking, freezing, curing, and irradiation) are included. The recommendations also address on-farm surveillance and control strategies. The ICT will also soon issue recommendations on serological testing for trichinellosis.

In brief, effective guidelines emphasise certain fundamental preventive measures:

1. Strict adherence to garbage feeding regulations, particularly refuse cooking requirements (bring to a boil for 30 min).
2. Stringent rodent control.
3. Prevention of pig and other livestock exposure to dead animal carcasses of any kind.
4. Proper disposal of pig and other animal carcasses (e.g. burial, incineration or rendering). This minimises infection risk for commensal wild animals.
5. Construction of effective barriers between livestock, wild animals and domestic pets.
6. Proper handling and disposal of wild animal carcasses by hunters.

It is clear from the experience of European countries that the mandatory inspection of pork is highly effective for the control of trichinellosis, particularly when coupled with trace-back procedures to identify farms with problems. The institution of careful animal management practices and long-term monitoring is highly important for permanent control. However, those countries relying heavily on post-slaughter control strategies (advice to consumers, regulation of commercial processes) can also achieve effective control, but such measures may have less effect on reducing the risk of the on-farm domestic cycle. This makes it important that veterinary services institute a program of surveillance of pig farms (by serological or tissue inspection means) to identify those farms requiring mitigation [95].

Because wild game is an important source of infection for both humans and pigs (*T. spiralis*, especially), all such meat should be considered as suspect and should only be consumed either after inspection by the trichinoscope or digestion method or after thorough cooking or curing. Some countries have instituted mandatory inspection of wild game, especially for wild boars (e.g. Germany, Italy, Russia). Others provide educational programs for hunters and consumers of game foods. For example, in the United States, the Montana Department of Fish, Wildlife, and Parks and the Montana State University Extension Service publish and circulate pamphlets to hunters on the dangers of eating improperly cooked bear meat. The Montana State University Veterinary Laboratory also offers free diagnostic services.

There have been few attempts to eradicate *Trichinella* from wild animal populations. As discussed above, an important factor in the epidemiology of trichinellosis in wild game populations is the habit of hunters to leaving the offal and carcasses of game and fur-bearing animals in the forests, where they serve as a source of infection for other animals. There has been demonstrated success in reducing the incidence of trichinellosis in a wild boar population in New Hampshire (USA) [51] by enforcing safe disposal of offal from wild boars shot by hunters. This suggests that transmission of *T. spiralis* in this game park was maintained primarily by scavenging of boars on discarded carcass remnants.

The idea of a vaccine for the control of trichinellosis in domestic swine herds has been attractive, and a candidate vaccine has been developed, utilising antigens of the newborn larval stage [96,97]. This approach could have application in the eradication of *Trichinella* in herds in which management strategies (above) have not been completely successful. The cost to produce such a vaccine for such limited use, however may be unacceptably high.

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